THESIS

GAMBEL OAK PRODUCTIVITY AND DEMOGRAPHY: AN OBSERVATIONAL STUDY OF FUNDAMENTAL ECOLOGICAL CHARACTERISTICS IN WESTERN COLORADO

Submitted by

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ABSTRACT

GAMBEL OAK PRODUCTIVITY AND DEMOGRAPHY: AN OBSERVATIONAL STUDY OF FUNDAMENTAL ECOLOGICAL CHARACTERISTICS IN WESTERN COLORADO

Gambel oak exhibits demographic and morphological variability across its range in the intermountain West. While broadly distributed, little is known about the basic ecological behavior of this species in Colorado ecosystems. We used an observational study to systematically describe variation in Gambel oak stand biometrics across a climatic moisture deficit (CMD) gradient on the Uncompahgre Plateau in western Colorado. Our analysis focused on parsing out differences in demographic characteristics including stand structure, age distribution, and productivity among varying levels of CMD with a 90-plot inventory capturing 2,312 tree measurements across a 200 mm range of CMD. To explore causal factors for variation in productivity, we used a mixed effects model derived from a systematic model selection process that identified predictors from a suite of biotic stand structure variables, and abiotic climatic and topographic variables. Metrics of tree size, stand density, and productivity varied systematically across the CMD gradient, where the driest sites had smaller trees, higher stand densities, and slower growth than wetter sites. In the driest sites, trees averaged 3.9cm of diameter at root collar (DRC) with mean densities of 9,000 trees per hectare contrary to the wettest sites where stems sizes averaged 7.5cm DRC with mean densities of 5,700 trees per hectare. However, regardless of variation in CMD, most stands were uneven-aged, as evidenced by uniform age proportions and ample regenerating cohorts of young stems across nearly all

plots. Within a 60km^2 study area across 500m of elevation difference, variables capturing climate and stand structure effects were the most predictive of productivity. A significant negative interaction between tree size and CMD indicates moisture limitation likely prevents trees on the driest sites sampled from attaining the larger sizes observed on wetter sites. Additionally, stands with high CMD were consistently younger than stands with low CMD, implying either more frequent stand-replacing disturbance in these locations or recent colonization of new areas. The demographic characteristics across all CMD levels indicate stands naturally achieve a more heterogeneous structure following about a century of growth. This suggests that management promoting multi-cohort stand structures could accelerate transition from homogeneous thickets to heterogeneous old forests. Given the variable growth rates across the CMD range, this would likely be most successful on wetter sites.

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CHAPTER 1: GAMBEL OAK PRODUCTIVITY AND DEMOGRAPHY: AN OBSERVATIONAL STUDY OF FUNDAMENTAL ECOLOGICAL CHARACTERISTICS IN WESTERN COLORADO

1.1 Introduction

Our ecological understanding of Gambel oak (*Quercus gambelii var.* Nutt.) demography and productivity is minimal despite the species' range and abundance. Gambel oak is a dominant cover type in 9.3 million acres of southwestern United States including New Mexico, Arizona, Utah, and Colorado (Kuchler, 1964). Throughout its distribution, it ranges from 5,000 feet of elevation in New Mexico and Arizona to 9,000 feet in Colorado and Utah (Harper et al., 1985). While many dominant, broad-ranging forest species have their foundational silvics described in the *Silvics of North America*, there is no profile for Gambel oak, despite the fact that the species covers 2.4 million acres of the 24.4 million acres of forested land in Colorado (Burns et al., 1965; Colorado State Forest Service, 2009). Throughout Gambel oak's broad distribution its morphology is incredibly variable. Near the center of its regional extent in the Coconino National Forest in central Arizona, the growth form often resembles a tree, where stems are frequently greater than 15 meters in height and have root collar diameters exceeding 20cm (Gholz et al., 1990; Landrum, 1993). By contrast, in the periphery of Gambel oak's regional extent, such as along the Western Slope of Colorado, stems rarely achieve such diameter and height metrics and instead appear on the landscape variably in the forms of shrubs and dwarf trees. Our minimal understanding of this species extends from morphology to basic aspects of demography and productivity. These characteristics are not addressed in "Gambel Oak in West-

Central Colorado", our most relevant piece of literature regarding the ecology of Gambel oak in the Colorado context, and thus there has been an impetus to revisit the fundamentals of ecological understanding for this species (H. E. Brown, 1958; Kaufmann et al., 2016). The abundance of Gambel oak in tandem with the lack of discrete ecological knowledge describing Gambel oak demography and productivity on the margins of its distribution provides impetus to study the species' fundamentals.

Expressed Gambel oak demography and productivity are variable at spatial scales as fine as a singular mountain, but no literature establishes the nature of this variation as it pertains to similarly scaled site condition drivers. Within the western Colorado context, the variation in Gambel oak stem form occurs roughly along an elevation band with shrubbier stems at the lower end of elevation and on steeper slopes and more tree-like stems at the upper end of elevation and on less steep slopes. (H. E. Brown, 1958). Since orographic processes influence fine scale climate that affects vegetative communities, we explore climatic and topographic causal factors for site level differences in age dynamics and stand structure (Ford et al., 2013; Levin, 1992; Whittaker, 1970). Gambel oak is an early seral, fire-adapted, deciduous woody perennial that is capable of three forms of asexual reproduction as well as reproduction via acorns (Huebner & Vankat, 2003; Jester et al., 2012; Larsen & Johnson, 1998; Lauver et al., 1989). Additionally, roughly sixty percent of Gambel oak's biomass is underground, allowing for its asexual modes of stump sprouting, rhizomes, and lignotubers to be especially resilient in post-disturbance environments (Tiedemann et al., 1987). Often occurring in monospecific patches. the vigorously sprouting, clonal, early seral, disturbance adapted nature of Gambel oak makes it hardy with respect to eradicating it with anything but long-term applications of soil-sterilizing levels of herbicide and repeated mastication (Epps, 1974; Jester et al., 2012). Reproduction is

predominantly asexual and most post disturbance regeneration occurs via sprouting mechanisms rather than acorn production (Kumar & Rogstad, 1998). These early seral organismal traits position Gambel oak to be well adapted to frequent and severe stand-replacing disturbances.

The intermountain west's regional climate is expected to favor more frequent and severe drought, greater overall aridity, and consequential fire regime alteration within the next century due to climate change (Baker et al., 2017; Cayan et al., 2010; MacDonald, 2010). Increasing severity of climate change will alter regional timing and availability of moisture, increasing the likelihood for drought and consequently increasing fire frequency and severity (Hurteau et al., 2014). This is expected to push dominant vegetative communities towards conditions outside of their historic range of variability (M. L. Floyd et al., 2000; Keane et al., 2009). In these new conditions, species that exhibit disturbance adapted traits such as Gambel oak's rapid asexual regeneration following high severity fire are advantaged over their non-disturbance-adapted counterparts (A. M. Barton, 1999; Guiterman et al., 2018; Harrington, 1985). For example, 75% of vegetation establishment the year following a stand replacing fire in the southern Rocky Mountains was a function of plant rhizomes (features of Gambel oak), culms, and stumps (Lyon & Stickney, 1976). In contrast, species that are sensitive to disturbance are unlikely to return as rapidly following stand replacing fires. Where stand replacing fires are more frequent, gradual transitioning through repeated disturbance from forest cover types to more fire-adapted shrubland is likely to occur (M. L. Floyd et al., 2000). The relative advantage of fire-adapted traits and early seral strategies for post-disturbance colonization or reinitiation is readily apparent in climate induced vegetation type conversion models (Notaro et al., 2007; Price et al., 2001). By understanding basic species level ecology for Gambel oak, we can make informed decisions for

management in the future where it is likely to be more widespread due to altered climatic conditions.

Outside of Colorado, knowledge of Gambel oak vegetation management strategies affecting demography and growth form are best understood in New Mexico and Arizona populations (Abella, 2008b; Ryniker et al., 2006). Across all populations, there are numerous ways to categorically parse Gambel oak cover into different types and there is a dichotomy in the literature for describing bole volume estimation in "shrub-form" versus "tree-form" stems (Clary & Tiedemann, 1993). Classification of demography and growth form is useful in a categoric sense to describe Gambel oak's variability and tie the different forms of Gambel oak to different intended management outcomes, such as promoting tree form Gambel oak for greater acorn production for wildlife management (Abella, 2008a). For instance, this utility would be directly useful for attaining preferred outcomes in managing oak communities given the species' high value for wildlife habitat as a food source and its importance as a primary habitat type for 17 species of "Greatest Conservation Need" (Colorado Division of Wildlife, 2006; Colorado State Forest Service, 2009; McCulloch et al., 1965). However, in the Colorado context, basic management-oriented knowledge including age structure and size demographics and trends in productivity are unavailable. By investigating fundamental ecological Gambel oak characteristics, we clarify the connection of management actions to desired outcomes.

Abiotic phenomena occur and interact with the vegetation mosaic in a spatially explicit manner. Top down abiotic drivers influence site condition allowing for interspecies competition to create spatial patterns in vegetation cover types. With a singular vegetation type, fine scale differences in topography and elevation alter population patterns of demography and productivity. As such, gradient analysis has been used to elucidate the importance of spatial

patterns in site condition as it pertains to both population metrics and interspecific occupation of landscape space in the vegetation mosaic. The use of ecological gradients has allowed for inference in causal processes that account for any variation along an observed gradient. Exploration of Gambel oak biometrics in Colorado specifically requires a framework that accounts for the state's orographic variability. Through studying productivity of Gambel oak in a gradient framework, novel linkages to directional changes in the abiotic aspects of site condition and climatic envelope come into focus. This additionally allows consideration of potential future Gambel oak productivity scenarios by relation to climatic envelope shifts as they're connected to the underlying causal gradient-based phenomena (Loarie et al., 2009). A gradient framework is an appropriate approach where the objective is to infer and describe how change in a continuous type of response variable is linked to a continuous change in a likely predictor variable (Gosz, 1992; Ter Braak & Prentice, 1988). Since variability in demography and productivity is often explained by site condition, and moisture is considered the most likely limiting component of site condition for Gambel oak (Abella, 2008a), our gradient is a proxy variable indicating spatially explicit moisture availability. This framework lends desired utility in rapidly assessing how biometrics of demography, including stocking, density, age proportion, and structure, are changing along a productivity gradient. Moisture nearly always covaries with elevation within the American West (Roe, 2005). By studying Gambel oak demography and productivity as it relates to this gradient, the efficiency of the study is enhanced, allowing for rapid comparisons of demographic traits as they relate to site condition characterized by moisture deficit. A gradient based approach to understanding these characteristics as they directly relate to changes in site condition along an elevation gradient is the most direct way of ascertaining the importance of site condition on productivity (Whittaker, 1967).

This project's objectives are to quantify biometrics of demography for Gambel oak on the western slope of Colorado and describe how they vary across the identified gradient approach. If patterns in biometrics exist within the chosen Gambel oak population, the gradient analysis will capture any directional change in these biometrics while also lending itself to interpretations due to the correlated nature of a landscape's abiotic gradients. This research question framework is two part: First, are there categorical differences for biometrics of demography and productivity across abiotic landscape gradients? Second, what are the factors causing observed patterns in demography and productivity across the sampled gradient?

1.2 Methods

1.2.1 Study Area & Sample Population

The Uncompahgre National Forest in the Western Slope region of Colorado is where the study design was established due to partnership with the United States Forest Service (USFS) and an abundance of Gambel oak distributed along an accessible elevation gradient spanning the entire elevation band of Gambel oak. This administrative National Forest boundary captures an 130km long plateau that sits oriented northwest to southeast and is distinct from the surrounding mountain ranges including the West Elks and the San Juans as well as the adjacent Grand Mesa (Case, 1991; Heyman et al., 1986). The geologic feature rises to 600m above the surrounding landscape and captures ecotonal ranges from sagebrush and pinyon pine to spruce/fir dominated subalpine forests (Rollins, 2009). The plateau influences local climatic patterns orographically and supports a mosaic of various vegetation cover types. From the lower slopes of the plateau all the way to its top, Gambel oak occurs in concert with other vegetation types as well as in monospecific "pure" patches. Topographically, the plateau is diverse with high elevation open park meadows on top of the plateau with deep gully drainages and steep sloped hills on the sides of the plateau eventually transitioning to gradual toe slopes. Climatically, the plateau is

characterized by the high elevation desert moisture regime the rest of the western slope of Colorado experiences. Much of the annual precipitation arrives in the form of snow throughout the winter and spring (Wang et al., 2016). A late summer monsoonal pulse of precipitation paired with a very low snow-water-equivalent is summed to about 250mm of water annually which characterizes this landscape as a semi-arid desert. Temperatures are below freezing on average through the winter for the weather station at Columbine Pass on top of the Uncompahgre Plateau. During the summer, temperatures frequently drop below freezing at night, but during the day, temperatures regularly exceed 35 degrees Celsius. This weather station is roughly in the center of the general study area with the farthest plots being ~15km away. The climatic and topographic conditions of the plateau served as the basis for establishing our gradient based sampling.

Defining the Population via GIS

The procedure for locating sample locations is described from data download to stratified locations of random sampling points within pure patches of Gambel oak with monospecific overstories. Plots were located randomly within a set of parameters chosen to ensure they would fall in the defined population of interest. The LANDFIRE dataset was used to extract raster grid cells that are attributed to represent areas of oak within the study area. These grid cell values were then transformed into a binary grid showing “oak” and “not oak”, and finally they were vectorized into a polygonal form. To account for the experienced variability following our pilot study, the resulting multipart polygon feature class was buffered from its perimeter inward by a linear distance of 50 meters as a function of the approximate distance patches of oak can be apart from one another and still be the same organism (Kumar & Rogstad, 1998). This broke the coarser and larger multipart polygon into finer pieces allowing for the population to be broken down once more. The resulting feature class was filtered into only the pieces that had an area

greater than or equal to 900 square meters. This process ensured that randomly located sample points would have decreased potential to have a false positive classification of oak due to the conservative restriction of the constrained spatial extent that random points were populated within.

Strata areas were chosen across the gradient of our proxy productivity gradient that had abundant oak coverage; Climatic Moisture Deficit (CMD). The maximum and minimum of the gradient encompassed a 200mm differential between 400mm of annual moisture deficit to 600mm of annual moisture deficit. By querying the layer associated with CMD, the strata were defined using two primary parameters. Firstly, they would span the range of values of CMD where oak occurred in abundance, and secondly, they would be accessible from maintained USFS roads. After choosing three strata across the gradient, a limiting 750-meter buffer was used to restrict the population to being within that proximity of accessible USFS maintained roads. The buffered linear distance values and the area criterion for restricting the population were chosen based off preliminary sampling experience from a pilot data collection trip.

The resulting population following these reductions was represented spatially by a feature class of the following conditions; Within "oak" as per the LANDFIRE dataset categorical classification of "*Quercus gambelii* Shrubland Alliance", 60 meters away from the edge of the LANDFIRE dataset's oak/non-oak boundary, only in polygons greater than 900 square meters of area, and within 750 meters of accessible USFS maintained roads. The feature class was clipped to three respective strata that spanned the variation in CMD in thirds to capture the range. This led to three strata; a high CMD stratum which was the most arid, a low CMD stratum which was the least arid, and a medium CMD stratum which was intermediately arid (Figure 1). One hundred random points were then generated in each stratum's restricted oak coverage. These

points were the spatial basis of the plot sampling unit in this design and allowed ample backup points to use if the plot locations were not acceptable in relation to the acceptance criterion outlined in the sample point protocol.

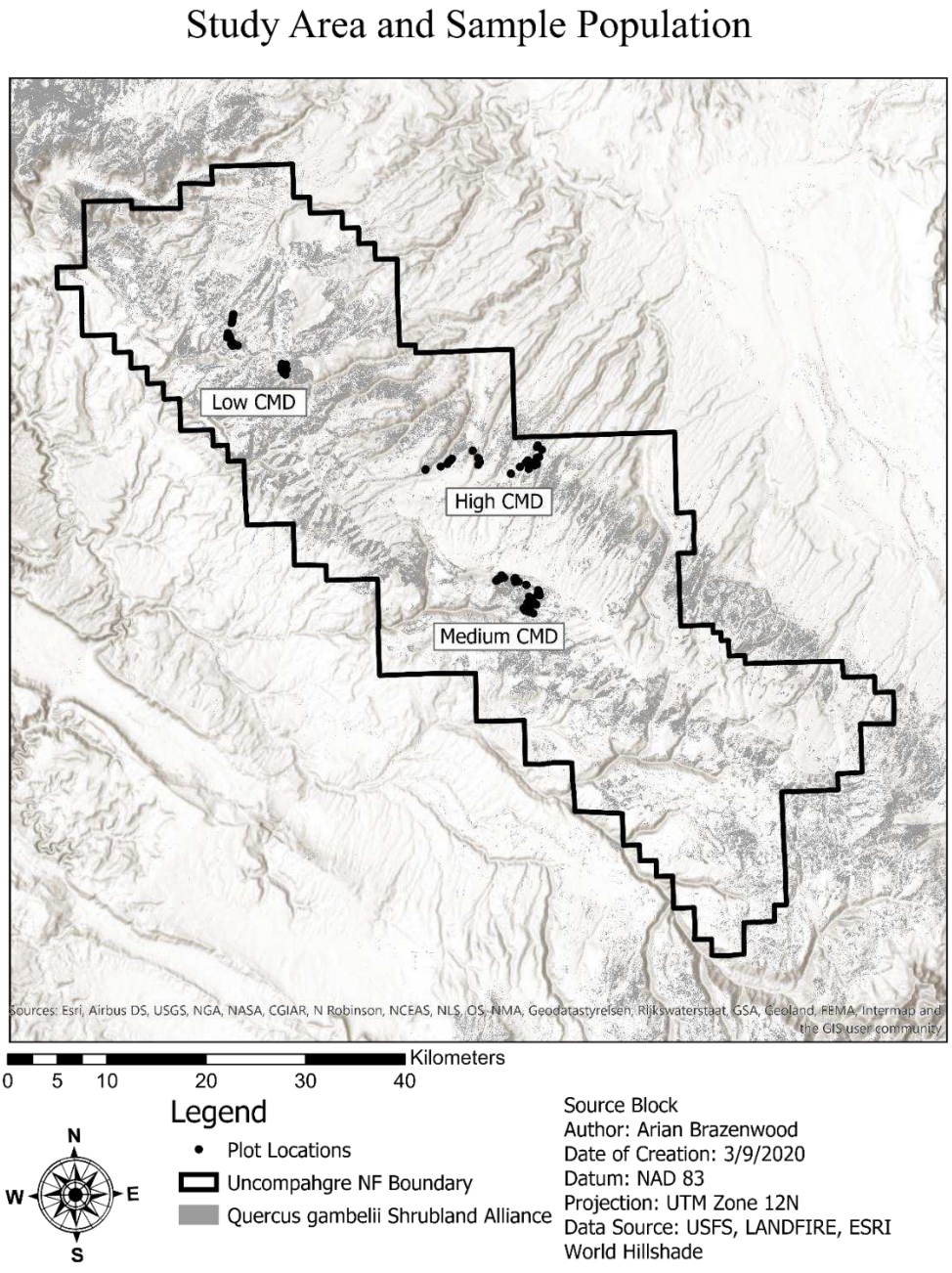

Figure 1. Map of the study area, which encompasses three parts of the Uncompahgre National Forest (Administrative Boundary shown) in which this Gambel oak study was executed. The study's stratified populations

are shown in NAD 83 UTM Zone 12N with the LANDFIRE Gambel oak existing vegetation coverage map and the ESRI World Hillshade for underlying topography and Gambel oak extent.

1.2.2 Study Design: Field Work

Sample Measurements and Data Preparation

At a plot level, the intention is twofold; to understand productivity the sampling needed to characterize size distribution and growth rates within the inventory. To understand demography, age distribution needed to be captured. A subsampling methodology was implemented to capture plot level characteristics including density, stocking, and the distribution of stem sizes; within this range of collected data, a systematic subsampling scheme was used to collect age data for assessing growth rates and age distributions within plots. After samples were processed, relevant metrics were calculated from the inventory in preparation for analysis, and plot topographic variables were calculated in a GIS framework.

Sample Point Protocol

First, each sample point needed to be vetted for a set of acceptance conditions. Since Gambel oak tends to grow in discontinuous patches, there needed to be enough quantity of oak stems that a belt transect of random azimuth could capture a minimum of fifteen stems, and the oak needed to be the dominant species in the canopy at the sampling point in question. For our purposes of dominance in species composition, the sampling point needed to be at least one and a half tree lengths from any other species in the composition of the canopy surrounding the sampling point to minimize the effect of interspecies biotic competition from influencing the observed stems. At a random sample point from the defined population, a belt transect of a random azimuth was used to capture the characteristics of the vegetation at the location. The belt transect from plot center was two meters wide, by a count of thirty stems long. It was variable

length on a per plot basis depending on the density of oak stems captured by the transect. A belt transect was terminated prior to reaching a count of thirty oak stems if it would leave an oak patch and travel more than twice the transect's maximum length without hitting any oaks, or if there was an abrupt change in topography that would allow stems in different abiotic conditions relative to plot center to be observed. This former reason was implemented to ensure observations were confined to a single patch such that a plot is representative of a stand. The secondary reason for termination ensured that data associated with each sample point would be representative of the topography and general abiotic condition attributed to the sample point. When the belt transect was terminated, whether as a function of minimizing the genetic/topographic variation within the sample or upon reaching a count of thirty stems, the transect length was recorded.

Along the transect, diameters were recorded at the root collar for all stems. For all stems, heights were recorded. In the field, an excel spreadsheet was used to determine, from the stems measured, which five stems constituted the maximum, minimum, median, first quartile and third quartile diameters measured. The subsample is a systematic sample based off the five-number summary of the range of diameter values measured at each plot. These five stems were cut at the root collar and slightly above (~3cm) the root collar to harvest cookies that would be taken back to the laboratory and measured using basic dendrochronology techniques.

At plot center, plot level observations were recorded. The slope percent and aspect azimuth were recorded. A categorical observation of relative slope position using a three-point scale was recorded where "1" meant the plot position was in a valley, a "2" meant the position was mid-slope, and a "3" meant the position was on a ridge. A soil core was taken at plot center

and depth to restriction was recorded for each plot. These metrics together summarized the fine scale abiotic situation of the plot.

1.2.3 Study Design: Data Processing

Lab Sample Processing

The collected stem root collar cross sections were processed for their ages using a basic aging technique. Samples were first prepared using a mixture of a stationary belt sander and a hand-held belt sander. The samples were sanded and then were hand polished to a 64-micron grit along the path from the vascular cambium to the pith in which they would be dated. Rings were counted by the decade underneath the microscope, then the quantity of decades were tallied. Following sample aging, a subset of 20% of the samples chosen randomly, but distributed evenly between strata were then resampled for their ages using a different path from their vascular cambiums to their piths. This resampled subset was used to assess sample processing error.

The distance from the vascular cambium to the inward edge of the 5^{th} and 10^{th} ring in was measured to assess the growth rate for each of the stems within a ten-year and a five-year period. This is termed Current Annual Increment (CAI) and was turned into a more interpretable number by converting the measured distance into a basal area of the cross-sectional area the stem has grown within the last five and ten years respectively. This was done by calculating a basal area of the stem with the measured distance removed from the stem's radius, then subtracting this area from the recorded total basal area of each stem. This likely overestimated the square centimeters of basal area CAI systematically due to the inclusion of phloem, phelloderm, and cork within the recorded total area of stem cross sections. In generating the response for the final model, the five year and ten-year periods were tested against each other in case the 2017-2018

drought had a noticeable effect on the growth rates of Gambel oak. In comparing the two final models via a type III ANOVA, there is no difference in information ascribed to the five-year relative growth rate verses the ten-year period relative growth rate response model. The five year is presented as the response rather than the ten year because they statistically show similar parameter estimates and interaction term significances and we were able to use more samples due to the number of processed samples that had ages under ten years. Of the 450 samples, two samples were lost. There were seven samples of the remaining 448 samples that had ages fewer than five years. These samples were not considered in the dataset of CAI values that were then used in the modelling framework. CAI was measured a second time for a subset of 20% of the samples chosen randomly while distributed evenly across the three strata. This recount was used to again assess sample processing error.

Data Preparation

The sampling spanned 90 plots in total with 30 plots per each of the three strata. Across the 90 plots, 2,312 stems were sampled (~770 stems per strata) with a subset of 448 stems systematically subsampled for the age/growth related metrics. Plot areas were calculated for all plots and stems per plot were normalized by plot area to find plot density. Additionally, basal areas were calculated for all stems and subsequently summed for all plots. This plot level summed basal area was used to arrive at stocking to account for variable plot size. Plot level aspect measurements were converted from a zero to three-hundred-and-sixty-degree range to an index of northness using the cosine function of their azimuthal angles. At the plot level, mean and maximum tree height, age, diameter, and basal area were summarized. Topographic variables were calculated through the ArcPro GIS interface using plot locations in relation to a 30m resolution digital elevation map (DEM). A geoprocessing tool was created to calculate

topographic position index (TPI) as a way of understanding relative elevation within the scope of a 90m horizontal distance radius neighborhood around each plot center. This tool was built in a parameterizable framework that allowed inputs to be varied such that we could find the neighborhood window that was best suited for scale of the effect of relative elevation on oak vegetation productivity. The tool calculates the mean elevation of all DEM raster grid cell values within the defined neighborhood, then computes the difference in elevation between the plot center elevation and the mean surrounding elevation. The range of the output is scaled to a 1 to -1 index for consistent comparison between plots, where the scaled values of 1 are indicative of being the highest point within the defined neighborhood window and values of -1 represent being perfectly in a depression relative to surrounding elevations. For example, a value of zero would indicate the stand's elevation is perfectly equal to the mean elevation of a three 30 m^2 raster cell neighborhood of the surrounding DEM pixels in the GIS analysis for derived topographic variables. Due to the difference in scale from the coarse resolution one square kilometer rasters of bioclimatic values and the continuous nature of these rasters, bilinear interpolation was used as the methodology for accounting for difference in scale, to garner more accurate estimations of bioclimatic raster values at plot locations. There was no significant difference when interpolation was compared to no interpolation in the final model output with a Type III ANOVA.

Estimating Sum CAI Values and Calculating Mean RGR values

With the goal of summarizing total additive absolute growth expressed as CAI at a plot level in mind, a mixed effects model was developed in R to estimate values of CAI for all stems that were not subsampled and processed. The model relates basal area to CAI with random effects for strata and plot. This model was developed using the relation of measured CAI values to measured basal area values. Since the design inherently captured the smallest and largest

stems of each plot, all estimated values for non-subsampled stems are interpolated, as they will always fall within the range of the five subsampled stems from each plot. The random effects for plot and strata are key as they allowed intercepts to vary categorically for each plot within the context of the variation that is attributed to each of the strata. This model relating basal area to CAI within the environment of the listed random effects was used to make estimates of CAI for all stems based off each stem's basal area as the input feature. Stem height was also considered as a potential predictor variable for CAI, but the model was stronger without it as it posed no significance and reduced the degrees of freedom within the model (Figure 2). With estimated values of CAI for all stems that were not subsampled, values were then added together to ascertain additive CAI at a plot level to understand plot level growth rates and be able to compare general absolute productivity. To account for the effect of tree size in estimating

productivity across all samples, the measured CAI was normalized by respective stem area of the subsample to derive relative growth rate (RGR) to serve as the response variable.

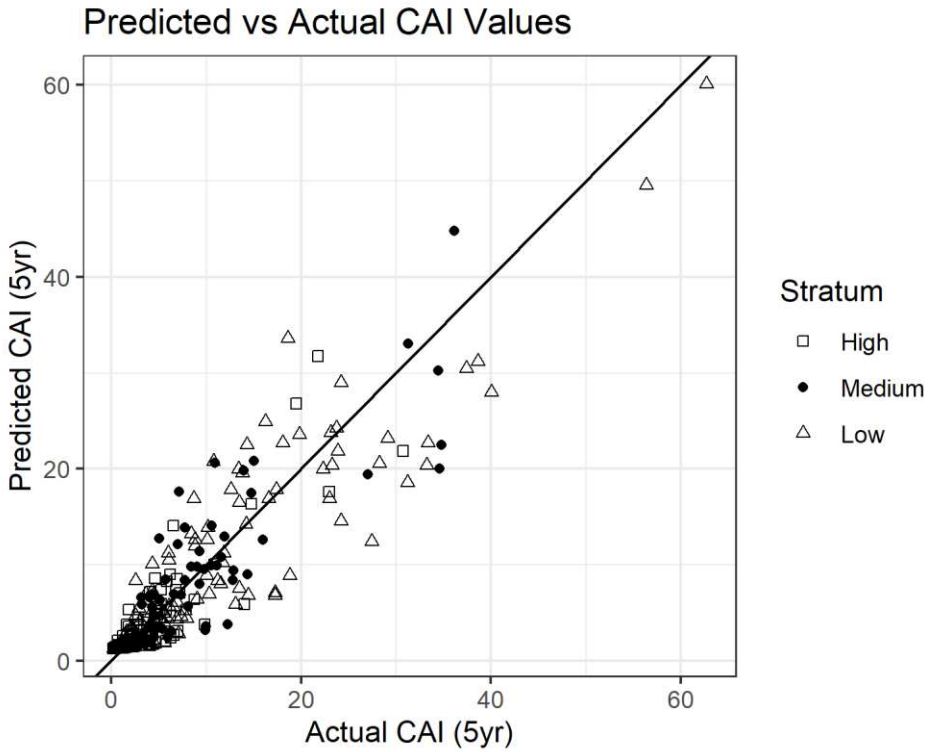

Figure 2. Scatterplot of actual measured values of CAI from the subsampled population of Gambel oak stems compared to the mixed effects model's estimate of CAI. This has a 1:1 line overlaid to visually assess accuracy of the model's estimated effects.

1.2.4 Analytical Approach: Demography

Utilizing the processed data and the derived plot/stand level metrics, we achieved our demographic objective in the analysis by summarizing the age structure and dynamics of pure Gambel oak per plot across the project. A proportion relating the range of ages at each plot location normalized by the maximum age of plots was calculated. The maximum age of stems within the plots was used because it functionally indexes the last stand-replacing disturbance the plot would have experienced. This relation provides insight into the nature of variability and

allows insight into the even-agedness or uneven-agedness that these stands could be exhibiting. The age proportions are shown by maximum observed age per plot to account for the temporal scope of Gambel oak on the plateau. This was done without the minimum stem of the subsamples per plot to account for the effect our sampling protocol has in potentially inflating extremes since our subsample always captured the smallest stem observed in each plot. To relate variability of structure to age distributions on a plot basis, we calculated a Stand Density Index (SDI) for each plot using both the traditional method and the additive method (Shaw, 2006; VanderSchaaf, 2013). The values of an SDI ratio begin at 1, which is indicative of a perfectly normal distribution of stem sizes across the sample unit, and increase indicating increasing non-normality. To interpret SDI ratios, higher values indicate more skewed or bimodal distributions of stems within each stand. In addition to generating age proportion and stand density structural figures, whether or not demographic metrics were variable across strata was tested in an ANOVA comparison of means by strata framework for stocking, density, age proportion, SDI ratios, mean basal area, and also the calculated plot level productivity metrics of both absolute and relative growth rates.

1.2.5 Analytical Approach: Productivity

To grasp the relative importance of factors pertaining to site condition, calculated metrics describing productivity and demography were analyzed as response variables in a mixed effects modelling framework with predictor variables relating to abiotic site conditions. Because sampling occurred in exclusively pure oak, the only biotic completion is assumed to be intraspecific, so structural metrics of mean stand tree size and SDI ratios were used as potential predictors of productivity. Since our methodology for delineating the sample population only allowed for pure oak, no consideration was given to predictors that described interspecific biotic

competition. An iterative dredge from the MuMIn R package for all parameter possibilities from a full model was then used in tandem with a likelihoods ratio backwards stepwise model selection process to reach the final model describing the relation between oak productivity (expressed as RGR) and abiotic variables.(K. Barton, 2019). Considered predictors were degree days above zero degrees Celsius, an interaction between northness and moisture deficit, an interaction between slope steepness and northness, an interaction between slope profile and moisture deficit, an interaction between slope profile and slope steepness, standalone northness, TPI (topographic position index), standalone slope profile, standalone slope steepness, number of frost free days in the growing season, mean stand basal area, Stand Density Index ratios, and climatic moisture deficit. The LME4 package was used to model the response variable of RGR with all considered potential climatic, topographic, and structural predictors with random effect of strata to account for the study design (Bates et al., 2015). The mean RGR per plot (n = 90) across the three strata references the systematically subsampled stems older than five years exclusively (n = 441). This response does not include the estimated values of CAI for the summation on a per plot basis. Plot was not included as a random effect because the response and all predictors are already summarized at a plot level.

1.3 Results

1.3.1 Demography Results

All biometrics except age proportion were significantly different between the high CMD and low CMD strata (Table 1). The significance threshold was consistently at a $p < 0.05$ across all tests and modelling outputs. Observed stems spanned sizes ranging from diameters of 0.6cm in the high CMD stratum to 40.6cm in the low CMD stratum. Sampled stand ages ranged from a mean subsample stem age of 9.4 years to 140 years. Stand density ranged from a minimum of

1,300 scaled stems per hectare to a maximum of 28,800 scaled stems per hectare. Variation of CMD and other considered abiotic and topographic variables were captured within the stratified design (Table 2). Data collection occurred in a single field season (2019).

Table 1. Biometric summary table including all measured and derived characteristics of Gambel oak summarized across plots on a strata level. Density and Stocking are scaled to the hectare to normalize for variable plots sizes. Relative Growth Rate has been scaled from square centimeters to square millimeters to highlight the directional change in values at a fine numeric scale. All values are means per respective strata with associated standard errors of the mean. Shared superscripts between strata for a biometric indicate no significant difference between strata means as evidenced by Tukey Honestly Significant Difference values for pairwise comparisons.

Biometric Summary Table		**Strata**		
Biometric	**Units**	**High CMD**	**Medium CMD**	**Low CMD**
Diameter	centimeters	3.9 +/- 0.43^{a}	4.8 +/- 0.64^{a}	7.5 +/- 0.60^{b}
Height	meters	2.09 +/- 0.05^{a}	2.26 +/- 0.06^{a}	2.71 +/- 0.06^{b}
Age	years	32 +/- 3.51^{a}	47 +/- 5.49^{b}	62 +/- 4.15^{b}
Density	trees per hectare	9270 +/-1040^{a}	7317 +/- 729^{ab}	5753 +/- 441^{b}
Stocking	BA per hectare	14.27 +/- 2.38^{a}	18.91 +/- 2.83^{a}	46.89 +/- 8.05^{b}
Age Proportion	range % of max	0.72 +/-0.04^{a}	0.73 +/- 0.05^{a}	0.73 +/- 0.04^{a}
Structure	SDI ratio	1.16 +/- 0.02^{a}	1.22 +/- 0.03^{ab}	1.25 +/- 0.02^{b}
Absolute Growth Rate	sum(cm^2/5yrs)	73.3 +/- 8.10^{a}	98.32 +/- 11.81^{a}	159.85 +/- 18.35^{b}
Relative Growth Rate	mean(mm^2/5yrs/BA)	3.75 +/- 0.34^{a}	3.27 +/- 0.22^{ab}	2.62 +/- 0.16^{b}

Descriptive statistics drawn from the sample population are represented by a sampled size of ninety plots. On average, we measured 25.7 stems per plot. The target number of thirty stem observations per plot was reached in forty-one of the plots. Nearly two thirds (fifty-eight out of the ninety) of all sampled plots had observed stem counts above the mean observed stems per plot. Only in four plots was a total number of stems observed at the minimum value of fifteen. Three of these four plots had very high basal area per hectare and very low stems per hectare relative to the sample population mean, thus characterizing them qualitatively as dwarf tree savannah type oak rather than the more common dense shrub type oak. The other minimum

count plot was not qualitatively savannah type oak, but rather it was ended because the random azimuth positioned it between a cliff and an open field.

Table 2. Variation for all abiotic predictor terms shown as mean values per strata with associated standard errors for the climatic predictors and ranges of values across all plots for the topographic predictors.

Abiotic Predictor Summary Table		**Strata**		
Abiotic Variable	**Units**	**High CMD**	**Medium CMD**	**Low CMD**
Climatic Moisture Deficit	millimeters	539.2 +/- 4.40	482.48 +/- 4.42	448.29 +/- 0.49
Number of Frost-Free Days	average # of days	176 +/- 0.73	163 +/- 0.80	160 +/- 0.21
Degree Days above 0° Celsius	#days>0 in thirty year normal	1808 +/- 11	1648 +/- 14	1483 +/- 2
Northness	Cos(Azimuthal Degrees)	Range (-1, 0.99)		
Slope Percent (range)	Percent	Range (1, 58)		
Slope Profile (Range)	1 to -1 index	Range (0.7, -0.79)		
Topographic Position Index (range)	1 to -1 index	Range (-1, 1)		

The ANOVA comparison of means approach tests the hypothesis that there is variation in demographic characteristics in at least one of the summarized means across strata. Gambel oak stems were generally larger, taller, and older with decreasing moisture deficit within the scope of the stratified sample (Table 1). Diameter and age across strata have a significant mean difference of 3.72cm and 29.88 years respectively between the high CMD stratum and the low CMD stratum. Stem height correlates strongly with both age and diameter trending towards taller stems with decreasing CMD (Figure 3). The low CMD stratum is significantly taller with a mean difference of 62.2cm for its pairwise comparison difference from the high CMD stratum. The medium CMD stratum is significantly different at the same threshold from the high CMD stratum in terms of age (15.65 years) and the low CMD stratum in terms of diameter (2.64cm) and height (45.7cm).

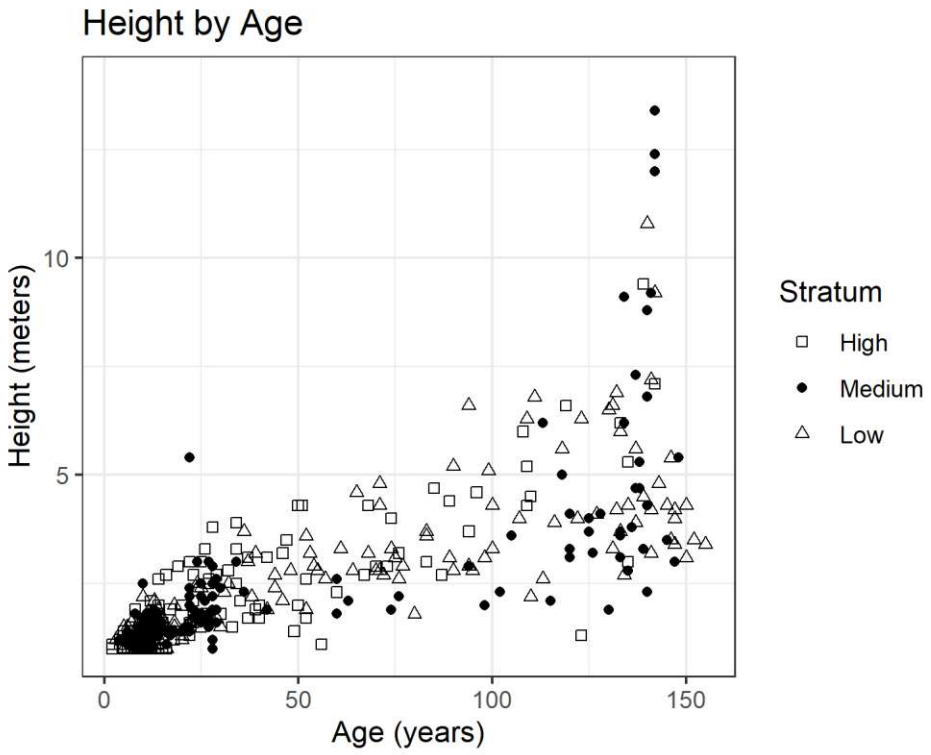

Figure 3. Height to age relation for all stems symbolized by strata (n = 2,312). Height growth rapidly achieves 1.5 meters within the timeframe of a decade. Then high increases with stem age typically achieving 5 meters after a century of growth. Taller stems are less frequent in the high CMD stratum.

For all stems with age data, the relation between diameter and age shows a positive trend with a tight relation that plateaus at roughly 150 years (Figure 3). The sample captured very few small and old stems. There were only two stems greater than 50 years old that were less than 5cm in diameter. While the lowest CMD stratum had most of the oldest stems, there were eleven stems older than 100 years captured in the subsample for the highest CMD stratum.

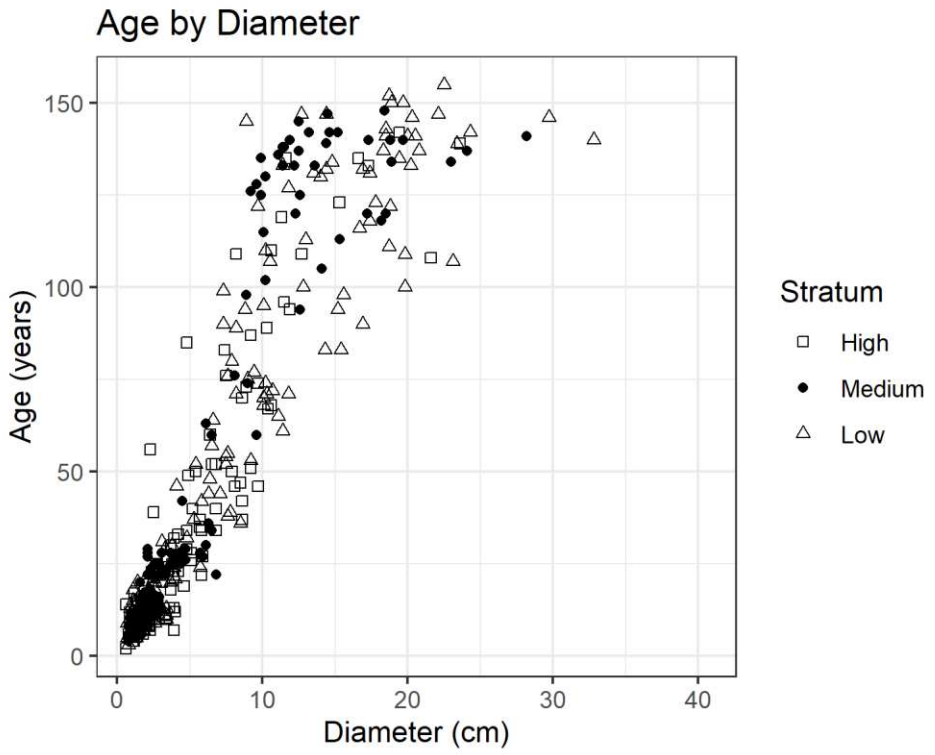

Figure 4. Age to diameter relation for all subsampled stems symbolized by strata (n = 448). Tight relationship has minimal small and old stems and has a plateau at roughly 150 years old.

Unlike diameter and age, density and stocking exhibited inverse trends across strata. This inverse relation between stocking and density across CMD points towards decreasing density with decreasing CMD and increasing stand stocking with decreasing CMD (Table 1). The increase in stocking paired with a decrease in density is afforded to the systematic increase of mean individual stem size with increasing CMD values. Mean strata density and stocking are shown scaled to the hectare to normalize for the variation of plot sizes resulting from stem density. However, we note continuous Gambel oak stands comprising an area of a hectare or more would be rare due to their patchy nature. Density increases with increasing moisture deficit. This difference is significant at a scaled 3,500 stems per hectare decrease between the lowest CMD stratum and the highest CMD stratum of the respective strata density mean. For the medium CMD stratum, no significant differences in density were observed compared to the

higher and lower CMD strata. By contrast, stocking increases with decreasing CMD. Between the high and low CMD strata, there was an average increase of 32.63m^2 of basal area per hectare for the low CMD stratum. Additionally, the Low CMD stratum has a higher mean significant difference of 27.99m^2 of basal area per hectare than observed in the medium CMD stratum. This indicates that the high and medium CDM strata are more similar in terms of stocking, however the low CMD strata is significantly more stocked than either the high or medium CMD strata (Table 1).

For age proportion and stand structure, similar age structure proportions were not significantly different across all strata but with variable and significantly differing structure via SDI ratios (Table 1). This is indicative of similar age dynamics in stands regardless of change in CMD values but with variable structure (Figure 5). The mean observed diameter across all stems is 5.32 +/- 0.1cm with a median of 2.9cm showing more than half of all stems observed are below the sample population mean. Within the sample's plots, more than half of all stems are below the sample mean indicating an abundance of small and presumably young stems given the tight age to diameter relation (Figure 4). Exceptions to this general condition are specific to plots that landed in young oak thickets and savannah type oaks where no variation in stem size was observed (Figure 5).

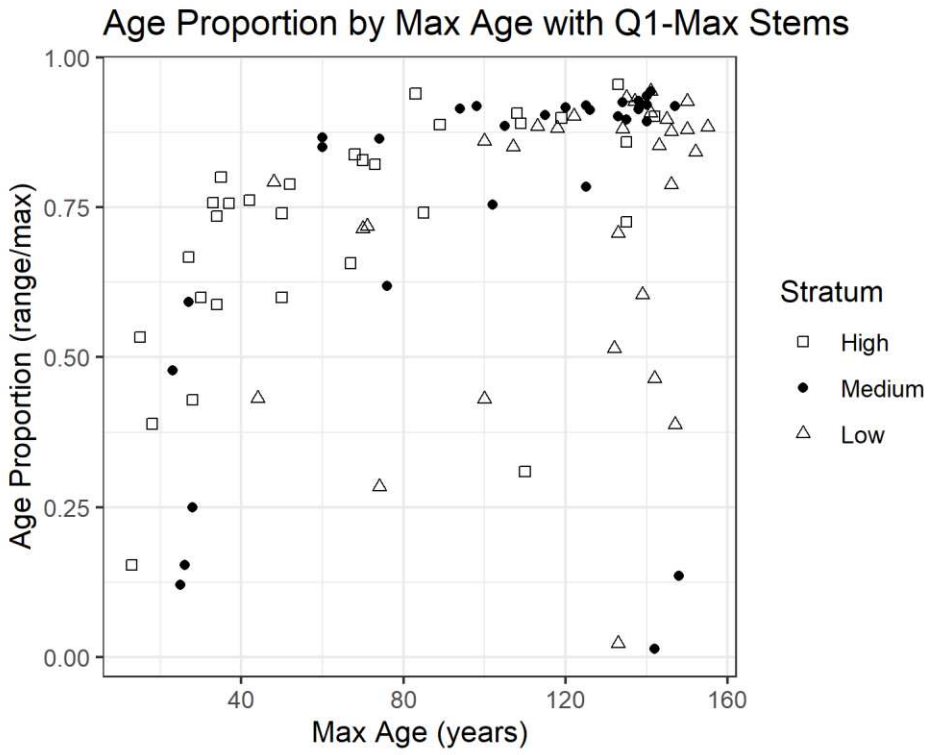

Figure 5. Age proportion of all plots (n = 90) symbolized by strata. The y-axis captures the range of stem ages from each plots subsample and scales the size of the range to the age of the oldest stem in the plot. The x-axis proxies time since last disturbance by referencing the age of the oldest stem in the plot.

Though age proportions are observed to be invariable across strata, structure as represented through SDI ratio values has significant categorical differences across the sampled moisture deficit gradient. The low CMD stratum has the highest mean SDI ratio which is significantly different from the high CMD stratum with the lowest mean SDI ratio. Regarding the structural metric, the medium CMD stratum did not exhibit significant difference from either the high or low CMD strata. With decreasing CMD values, SDI ratios increase with a corresponding significant increase of 0.09 percentage points of SDI ratio values between the high CMD and low CMD strata. This shows that with decreasing moisture deficit values, stand structure becomes more non-normally distributed. Alternatively, as moisture deficit values increase, stand structure becomes more normally distributed. Age proportion and structural pairwise comparisons across strata in tandem show similar uneven agedness but differing

normality of size distribution across the moisture deficit gradient despite the similar trends of age and diameter (Figure 6).

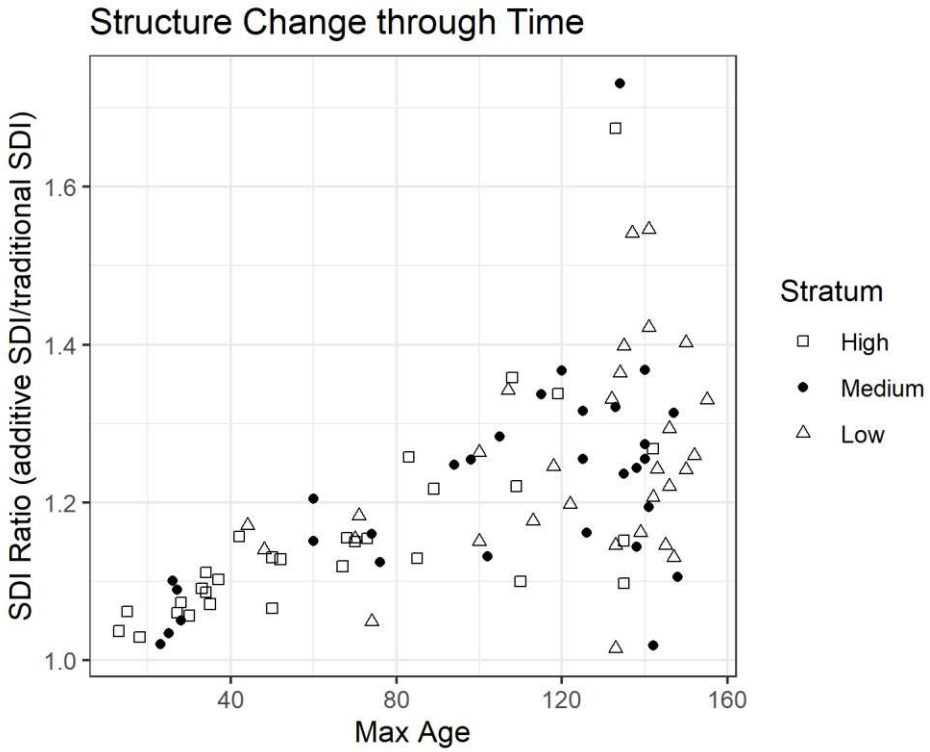

Figure 6. Structure as represented by SDI ratios show increasing non-normality with increasing plot ages. The x-axis proxies time since last stand replacing disturbance with the age of the oldest stem in the plot, and the y-axis captures the ratio between traditional and additive stand density index methods. This figure also shows the systematic difference in either disturbance reinitiation or establishment across strata given the minimal young Low CMD stratum plots and the minimum old High CMD stratum plots.

1.3.2 Productivity Results

Relative and absolute growth rates differ significantly in an inverse manner across strata capturing the relation between moisture deficit's consequent effect on productivity (Table 1). Relativized growth rate accounts for the effect of stem size on productivity while normalizing by stand area accounts for the effect of stem density. Absolute growth rate contrasts relative growth rate with an inverse relation that persists when density is accounted for when stands are normalized by area. Between the high CMD stratum and the low CMD stratum, there is an increasing difference of 86.54cm^2 of absolute growth expressed as the summation of stand basal

area growth within the last five-year period. Between the medium CMD stratum and the low CMD stratum, there is an increasing difference of 61.52 cm^2 of absolute growth rate. Since basal area is indicative of stem biomass production, relative growth rate serves to account for the effect of size on productivity for inference on growing space use in terms of efficiency for comparison across spaces. Relative growth rates are only significantly different between the high and low CMD strata. Mean relative growth rate values have fine numeric scale and have been scaled from their referenced plot area to hectares. With this scaling, there is a significant decrease of 7.05 units of current annual increment per unit of stem area per hectare when comparing the high CMD stratum to the low CMD stratum. Relative to their own size per the RGR normalization, stems are growing more rapidly in the high CMD stratum, however the greatest quantity of cross sectional basal are per stand has been produced in the low CMD stratum in the last five-year period. The productivity analysis indicates patterns in structural biometrics and abiotic climate predictors that describe the variation in relative growth rate for Gambel oak along the stratified gradient. Specifically, through the mixed effects modelling framework, relative growth rate is predicted by stand mean basal area, the SDI ratios of each stand, and climatic moisture deficit along with an interaction term tying the directions and magnitudes of climatic moisture deficit and stand mean basal area together (Table 3). These traits remained in the model at a chosen threshold of $p < 0.05$ after backwards stepwise reduction from a full model (Table 4).

Table 3. Order of removal for all considered predictor terms. Ranked by retained predictors first, then descending by the order of removal in the backwards pairwise approach of the model selection process. Rationale for removal briefly summarized with expected direction of each effect included.

Order of Removal	Variable Name	Units	Rationale for Potential Interaction Term expected Directionality	Expected Direction of Effect
not removed	Mean Tree Size	cm^2	Fundamental effect of stem size	negative
not removed	Interaction Term	N/A	Effect of moisture limitation on stem size	negative
not removed	Stand Density Index	%	Intraspecific Competition via Structure	negative
not removed	Climatic Moisture Deficit	mm (low = wet, high = dry)	Moisture limitations at a climatic scale	negative
12	Number of Frost-Free Days	ave annual days/30yr_norm	Average Annual Growing Season duration at a climatic scale	positive
11	Slope	%	Moisture retention and erosion	negative
10	Concavity/Convexity of slope surface	(+1= more concave, -1 = more convex)	Proximity to water table and effects of flow rates of surface runoff	positive
9	Topographic Position Index	scaled: (+1= highest point, -1 = lowest point)	Moisture accumulation/loss via surface run off	negative
8	Converted Aspect	(+1= more north, -1 = more south)	Topographic effect on angle of incoming solar radiation	positive
7	Interaction Term	N/A	Northness positive effect in concave slopes, negative effect in convex slopes	N/A
6	Interaction Term	N/A	Growing season duration negative effect in high CMD, positive effect low CMD	N/A
5	Interaction Term	N/A	More pronounced effect of profile with increasing slope	N/A
4	Interaction Term	N/A	Profile positive effect high CMD, negative effect at low CMD	N/A
3	Interaction Term	N/A	Variable slopes solar incidence	N/A
2	Interaction Term	N/A	Northness positive effect in high CMD, negative effect in low CMD	N/A
1	Degree Days above 0 Celsius	#days/30yrnormal	Freezing Temperatures experienced at a climatic scale	negative

The scaled mean basal area of each plot contributes the most information of any singular predictor in this model given its sum of squares value (Table 4). The scaled parameter estimate is negative indicating a decreasing effect on relative growth rate with increasing mean stand stem size. The next most informative piece describing the variation in relative growth rate is the interaction term between scaled climatic moisture deficit and the mean plot/stand basal area. The -0.007159 parameter estimate for this interaction term indicates that as the scaled numeric values of either parameter increase, the negative parameter estimate for the other predictor is amplified by the quantity of the parameter estimate for each whole unit of increase. For instance, a 1 unit of scaled increase in climatic moisture deficit results in a shift of the parameter estimate of scaled plot/stand mean basal area from -0.009639 to -0.016798 thus amplifying the negative effect of increasing tree size on relative growth rate. The SDI ratios were the next most informative parameter estimate with a negative sign indicating a decreasing effect on relative growth rate where increasing values of SDI ratios indicate non-normality of stand size structure. The parameter estimate for climatic moisture deficit is negative showing a decreasing effect on relative growth rate with increasing moisture deficit relative to the scale mean of zero. This parameter is insignificant but kept in the model due to the rule of hierarchy given its presence in the significant interaction term.

Table 4. Final model parameter estimates, standard errors and associated significances. The directions of the predictors are indicated by the signs of their parameter estimates while their importance is indicated by their Type III ANOVA sum of squares model ranking. All parameter estimates are scaled such that the predictor's mean is equal to zero because all tested predictors from the comprehensive final model are on differing scales.

Scaled Final Model Summary			
Fixed Effects	**Estimate**	**Standard Error**	**P-value**
Intercept	0.029702	0.00199	0.016526
Mean Tree Size	-0.009636	0.001555	2.03E-08
CMD:Mean Tree Size	-0.007159	0.001939	0.000475
SDI Ratio	-0.003139	0.001279	2.03E-08
CMD	-0.001639	0.00187	0.426574

1.4 Discussion

1.4.1 Demography Findings

Insights into the relations between characteristics of site condition and Gambel oak morphology are key to building knowledge on a species with large extent that inhabits variable regional climate and topographic conditions. This study has described invariable age structure and has shown that directional variation in stocking, density, growth rates, and stand structure are captured in a gradient analysis. This positions us to consider the drivers of observed characteristics.

Age to Diameter Relation

Our analysis has captured a continuous and tight relation between stem size and age over the full extent of sampled oak. We are in a position to improve upon previous work regarding the species' morphological variability. The best qualitative categorical characterization of Gambel oak morphology by shrub and tree form stems was implemented across varying locations representing the site conditions associated with each form (Clary & Tiedemann, 1993). Since we sampled oak stems across a gradient that captures site conditions described in the sampling

methodology Clary & Tiedemann (1993) used, our data set encompasses their respective age to diameter relations (Clary & Tiedemann, 1993). In their work, shrub form oaks were characterized by a site described as being on slopes of up to 40% steepness and tree form oaks were in sights with concave slope positions in locations that favored moisture accumulation. The high CMD stratum in our study is qualitatively more like sites where they measured shrub form stems where conditions were more arid and plots often were on steep slopes and our low CMD stratum is qualitatively more like the sites where they measured tree form stems where conditions were generally flatter or were in or near drainages. Across all strata, stem ages are best described by stem size (Figure 4). However, there may be instances of suppressed Gambel oak stems in the understories of other dominant cover types, so this finding is limited in scope of oak age dynamics in pure Gambel oak as described within the sample point criteria. This relation lays the groundwork for estimation of ages for stems within any population with similar ranges of abiotic conditions to our sample population.

Age Proportion

Within our sample population, all stands exhibited recent cohorts of young stems indicating continuous regeneration regardless of moisture deficit variation. This puts Gambel oak stand structure into an uneven aged framework due to the observed pattern of increasing age proportions with increasing stand ages within sampled stands that have abundant younger stems across all plots (Figure 5). Recently established stands tend to show a more even age distribution assuming measured stems are a good proxy of the last stand replacing disturbance. As time progresses and stands mature, patches will likely continue to sprout stems frequently via asexual means since the age proportion between the range of ages normalized by the maximum age increases with a stand's maximum age. Notably, there is no significant difference in age

proportion metrics across strata meaning that the uneven age structure is characteristic of Gambel oak regardless of climatic moisture deficit.

SDI Shift

Stand structure referenced by SDI ratio also shows a positive trend with increasing stand age. As SDI ratios indicate the normalness of stem diameter distributions per sample unit, the interpretation is that over time, the diameter distribution of pure Gambel oak stands become more non-normally distributed (VanderSchaaf, 2013). Since age and diameter are strongly correlated, the non-normally distributed diameters reflect the non-normal shape of age distributions with increasing stand age as well. The effect of non-normal size distribution is tied directly into the interpretation of stand age dynamic unevenness and continual regeneration as a result. At the time of establishment, stand size structure is more normally distributed, through time, the distribution shifts toward either a skewed or a bimodal distribution of sizes if an understory and overstory develop. The relation between stand age and structure allows for insight into stand history through assessing stand structure (Adams & Ek, 1974). The greater the SDI ratio for a stand, the older it likely is, allowing time for observed structures to develop (Figure 6). Gambel oak stands are shown to become increasingly uneven aged and their diameter distributions become more non-normal through time, and stands can be expected to follow these trends in the absence of treatments or stand replacing disturbances. Our documentation of landscape scale disturbances in this region is limited to the last 150 years, however intermittent small-scale disturbances are likely to reset development across the range of stands in the study region (Baker et al., 2017). The patterns of establishment or reinitiation across the imposed strata are also evident in the age proportion and stand structure figures. For the high CMD stratum, 2/3 of stands are fewer than 80 years old whereas for the low CMD stratum, 2/3 of stands are greater

than 120 years old (Figure 6). The medium stratum spans this pair of extremes represented by the highest and lowest strata. We can only speculate at potential causes of this systematic variation in age difference across our study design. The explanation for variation lies either in differences across the moisture deficit gradient tied to disturbance intervals or alternatively competitive exclusion and cover type conversion. The former potential explanation is that disturbance intervals are much more frequent in the lowest stratum relative to the highest stratum. This would indicate that along the moisture deficit gradient, there are climatic or topographic processes setting variable frequency of stand replacing disturbances (P. M. Brown & Wu, 2005; Swetnam & Betancourt, 1998). Increased disturbance frequency of fire in the driest High CMD stratum which is potentially more fire prone would explain why stands are more commonly younger there while still having pockets of older stands that have survived throughout the last 150 years. In the low CMD stratum, older stands are more common because they experience stand replacing disturbance less frequently allowing for greater periods of time for stands to mature and differentiate in both structure and age form. Alternatively, the explanation could tie into interspecific competition between pure Gambel oak and other cover types. In the low CMD stratum, space is more tightly occupied by communities other than Gambel oak where site condition is good. Because ecotones are shared with species that create dominant overstories such as aspen, ponderosa pine, and Engelmann spruce, there are few opportunities for Gambel oak to expand into those understories since it is shade intolerant (Hardin, 1960; Malanson et al., 1992). As such, initiation of new stand likely happens when a disturbance creates an opening in the cover type of some other dominant species (Putz & Canham, 1992). Barring that, Gambel oak is possibly saturated in its realized niche in the low CMD stratum. By contrast in the scope of this possible explanation, in the high CMD stratum, Gambel oak is establishing in novel areas,

hence the abundance of younger stands. Rather than stand age being exclusively a proxy for the last stand replacing disturbance reinitiation, the age could be interpreted as a time since cover type change via establishment. This could be in terms of acorn dispersal via wildlife or through gradual expansion of existing Gambel oak stands through asexual reproduction. These explanations can be explored in future studies built upon the fundamental knowledge this project has created. Despite causal factors, the pattern has been documented in the study and implies systematic difference in factors relevant to patterns of Gambel oak regeneration/dispersal/disturbance-ecology that needs to be explored further for informing ecologically informed decision making.

1.4.2 Productivity Discussion

The described final model outcome yielded interpretable and discrete ties between Gambel oak productivity and tested climatic, structural, and topographic predictors. A final model with significant predictors and interactions at $p < 0.05$ and a retained insignificant predictor was as arrived at in the mixed effects model framework (Table 4). The model's random effect allows for variable intercepts to account for the induced skewedness of dependency of samples within strata. With variance explained by the random effect, inference on predictor terms is directly a function of the fitted linear regression's parameter estimates and sign directions (positive/negative) as well as the implications of insignificant terms. No topographic predictors were retained in the final model, however two structural predictors, one climatic predictor, and an interaction term between two of them were kept (Table 3).

The mean tree basal area at a plot/stand level was the most significant and explanatory of tested factors for the variation of the mean relative growth rate. The predictor was used to index the importance of mean tree size summarized to the stand because stem size is expected to be

explanatory of growth metrics. Mean relative growth rate as we have calculated it is an imperfect proxy getting fundamentally at the stem's ability to capture light. An extremely precise approach would have included a methodology that destructively sampled to finer pieces or did carbon accounting work to get at a true productivity via efficiency of photosynthetic components (Landsberg & Waring, 1997; Malhi et al., 1999; Phillips et al., 1998). However, our methodology for measuring and relativizing CAI per unit of basal area is coarse but still functional with our more extensive sampling approach (Mitchell, 1975; Somogyi et al., 2007; Waring, 1983). Since productivity is linked to age and size in terms of efficiency and those biometrics are correlated, mean tree basal area was expected to indicate the physiological upkeep that comes with size and its interplay with productivity. The negative direction of the mean tree basal area implies that relative growth rate decreases as stands are populated with larger stems, therefore capturing a declining efficiency of growth with increasing size (Enquist et al., 1999; Mencuccini et al., 2005; Ryan et al., 1997; Weiner & Thomas, 2001). This contrasts the alternate expectation that growing efficiency increases with increasing stem size in vascular plants (Day & Greenwood, 2011; Stephenson et al., 2014; Steppe et al., 2011; Wykoff, 1990). This is likely due to the significant negative interaction term with CMD pointing towards moisture limitation to productive efficiency that is amplified with larger stem size in this xeric context. Gambel oak stem growth rates are well explained by their size alone with the largest absolute parameter estimate associated with its descriptive power (Table 4), but the explanation is enhanced with both SDI ratios and CMD for understanding the variability of productivity.

The parameter estimate for the SDI ratios predictor was expected to have a negative direction relating to mean relative growth rate because decreasing stem size normality in stand structure can create situations where intraspecific competition is increasingly asymmetric

therefore reducing the summarized mean relative growth rate. The systematic nature of our subsample captures the mean relative growth rate across the five-number summary of sizes. As the SDI ratio increases for a plot indicating greater non-normality, the subsample captures stems in more disparate size classes. Because of this, structure differentiates and the mean relative growth rate across the subsample is spanning stems that are both prominent members of an overstory as well as recent regeneration in the understory. Mean basal area of the standalone already points towards the importance of stem size, but the significance of SDI ratios implies that stem sizes of stand in conjunction to stand structure is more explanatory of variation in pure Gambel oak productivity. With larger stems in non-normal stands, resources are allocated to support physical structures, root growth, and other non-bole dimensions of trees (Smith & Long, 1989). Conversely the smaller stems may also have reduced relative growth rate with increasing non-normality as a function of asymmetric competition such as shade intolerance in the closed canopy that comes from differentiated stand size classes (Pretzsch & Biber, 2010). The negative effect of both structure in terms of SDI and mean basal area point towards higher mean relative growth rate in stands that are more normally distributed and have smaller stems.

Building upon the explanatory power of stand structure to describe mean relative growth rate, the climatic condition of stands and the interaction between climate and stand structure elucidates further insight. Despite being the only significant climatic predictor, CMD was an insignificant parameter for explaining the variation of relative growth rate alone. However, CMD's modelled effect on relative growth rate was negative, which matched expectations of the importance of moisture limitation for plant growth in arid environments. Despite the insignificance, it was retained in the model due to the rule of hierarchy with interaction terms. Independently, it contributed the least amount of information to the final model. The interaction

between climatic moisture deficit and mean stand basal area was, by contrast, very informative and significant. This interaction term parameter estimate was consistent with our expectations with a negative estimate and encompasses both stand structure and CMD together in describing variability of relative growth rate for Gambel oak within our sampled population. The negative parameter estimates for the significant interaction between stand mean basal area and climatic moisture deficit can be thought of as a further reduction in in the relative growth rate decrease associated with increasing CMD with increased mean stand basal area. This indicates increasing moisture limitation exacerbates the negative effect of being a larger stem in terms of productivity within our modeling environment. This is consistent with general understanding that moisture limitation reduces stem productivity (Gholz et al., 1990). More broadly, with greater size, larger quantities of limiting resources are needed to upkeep and maintain physical structures (Kempes et al., 2011; Li et al., 2018). This interaction term highlights the importance of climate at the site level interacting with mean size to describe this phenomenon in our sample population of pure Gambel oak.

The range of tested topographic predictors including northness, slope steepness, slope profile and topographic position index and their interaction terms were all null predictors of relative growth rate in the mixed effects model framework. Given the longstanding ecological understanding of the interplay between vegetation and the abiotic components of the environment including topography, it was surprising when the model selection process removed them from the model (Armesto & Martinez, 1978). Slope steepness was expected to have a negative effect on the relative growth rate of Gambel oak due to the increased magnitude at which erosional processes occur on steeper slopes lending to sediment removal as well as the decreased capacity for soil to retain moisture (Cerdà, 1998). Northness was expected to have a

positive effect on relative growth rate for Gambel oak due to its importance regarding snow persistence into the growing season on northerly slopes and a respective negative effect of aspect on southernly slopes due to solar angle of incident (Kirkby et al., 1990; Kutiel & Lavee, 1999). Stems growing on more northernly slopes would likely have snow cover persistence further into the growing season and thus would benefit from moisture not accounted for exclusively by CMD predictor The tested interaction between CMD and northness was expected to have a positive parameter estimate to capture the expectation that increasingly northern slopes had reduction on the expected negative effect of climatic moisture deficit on stand mean relative growth rate. However, the aspect predictor and its interaction were insignificant. Slope profile exacerbates slope steepness and indexes concavity and convexity of the slope surface relative to surrounding elevation values of the DEM. It was expected to have a positive parameter estimate due to the variable distance between slope surface and water table proximity being important given Gambel oak's xeric clonal nature. Slope steepness and slope profile were considered in tandem as interaction terms to each other as well as to northness and CMD because of their relevance to hydrologic process via overland flow draining to create areas of variable moisture availability within similar CMD values. The interaction between northness and slope steepness in particular was expected to have a negative parameter estimate where increasing values of slope steepness would amplify the effect of northness due to more potent angles of solar incidence. These slope related predictors and interactions were insignificant predictors of relativized growth rate despite expected parameter effects. In addition to slope characteristics and aspect, topographic position index was tested for significance in describing the variation in relative growth rates due to its value in indicating potential hydrological implications of drainage explaining stand mean relative growth rate's connection to relative elevation (De Reu et al., 2013). This parameter was expected

to have a negative parameter estimate indicating the positive effect a topographic depression would have on relative growth rate due to presumed moisture catchment. While the descriptive ability of topographic position index to describe variation in the response within the mixed effects model framework was superior to any of the other derived or measured topographic variables, it was still cut from the final model in favor of exclusively structural and climatic predictors. Despite these expected relationships, stand structure was most influential in determining growth rate in our study area.

The temperature oriented climatic components of the productivity analysis were degree days above zero and the number of frost-free days in the growing season. The literature associated with Gambel oak catkin formation notes strong inability to deal with freezing temperatures (R. P. Neilson & Wullstein, 1980). Late spring freezes are considered detrimental to Gambel oak reproduction (R. Neilson & Wullstein, 1983). Within our own experiences, we've observed late spring frost-induced top kill of Gambel oak stems and expected stem productivity to be detrimentally impacted by decreasing temperatures or shortening growing seasons. However, in our study the temperature component and the duration of the growing season were not shown to be significant predictors. This disconnect from our expectations could be because there is a departure in the effect between temperature productivity compared to temperature and reproduction. Additionally, this could be an issue of spatial scale of the temperature data compared to the plot level temperature dynamics experienced by stems. This also may be an issue of temporal resolution of our predictor data regarding the observed top kill on Gambel oak stems associated with a late spring freeze. Since the ClimateWNA PRSIM-derived datasets reference the 1961-1990 annual thirty year normal, the known effect of freezing late spring temperatures could be washed out of the average quantity of days above zero per year as a

function of their downscaling methodology (Wang et al., 2016). Given the intolerance to freezing temperatures Gambel oak has exhibited, the expected effect was that increasing the quantity of days above zero degrees Celsius would have an overall positive effect on relative growth rates. This could also have been relatively less informative in describing relative growth rate information compared to the sheer duration of the growing season on average as expressed by the number of frost-free days in the growing season predictor. Growing season duration correlated inversely with CMD and was expected to have a positive effect on relative growth rates. Growing season duration limits productivity severely for deciduous species like Gambel oak. Since the stratified gradient has an inverse relation between growing season duration and temperature, it was expected that their dynamic would highlight what is more descriptive in the model selection process. The effect of moisture deficit is much more explanatory of relative growth rate within the model framework, and the predictor describing growing season duration dropped out of the selection full model.

While significant relations describing relativized growth rate where characterized by our modelling output, consideration should be given to the constraints of our experimental study design. The way in which the sample population was delineated required that random sampling locations be exclusively in “pure oak” as defined by our constriction and extraction of attributed oak cover from the LANDFIRE dataset. Our productivity analysis looks at pure oak exclusively, and so there is the potential that we are systematically not sampling across types of situations of topographic predictor variables where “pure oak” is competitively excluded by cover types that we did not sample in. For instance, our sample didn’t capture slopes wherein the slope is too steep for oak to persist or the slope is flat enough that other species are relatively advantaged in terms of biological competition because our initial sample delineation would have preemptively

removed those conditions. While it is necessary to limit the scope of our conclusions to pure oak cover for the purpose of this project, the general interplay between topography and local climate needs to be considered further in context of biotic competition as it shapes distributions of species given our work is intentionally exclusive of intraspecific influence on Gambel oak productivity. When contextualized, it may be appropriate to attribute our results of pure Gambel oak relative growth rates to systems of pure Gambel oak beyond our sample population. While the top down drivers of local climate and stand structure are overwhelmingly indicative of productivity, the effect of fine scale topography may have been insignificant due to regional topography's inherent influence on local climate. A study design looking explicitly at topography without change in landscape scale climatic variables has the potential to find the expected relations. Additionally, the importance of soil was considered but not investigated. Given the variability in Gambel oak growth across the sampled strata, the effect of soil as relating to Gambel oak morphology is likely more relative at both coarser and finer scales than a landscape given the ways in which soil is variable. At scales coarser than a landscape, parent material, timeframes of formative processes, and patterns in precipitation/temperature/climate influence soil more significantly than at the scale of a singular plateau (Pendleton & Jenny, 1945). Conversely, at scales smaller than a landscape, soil characteristics such as mineral content, moisture availability, and soil texture are variable within ranges of meters rather than kilometers. An investigation of the properties of soil as they relate to demography and productivity would need to be explicitly studied as patterns would likely be found outside the spatial resolution of a landscape alone (Meentemeyer & Box, 1987). Because the spatial scale of our response was coarser in spatial resolution and we chose to look at dynamics between climatic parameters along a gradient as they relate to Gambel oak, we are unable to fully discount the

importance of the removed topographic variables exhaustively nor the full importance of soil since it was not investigated pertaining to the objectives of this study.

1.4.3 Climatic Implications & Management

The demography and productivity analysis in tandem garner insight into the behavior of this species in the Colorado context that positions us to consider broader climatic and management implications of the findings. The modelled sensitivity to CMD through the significant interaction term indicates sensitivity towards the landscape scale effect of climate. If climatic conditions affecting CMD favor greater interannual variability promoting aridity, Gambel oak is situated to potentially expand into novel areas given its xeric ecological profile. The demonstrated increase of relativized growth rate with aridity due to the CMD interaction with mean stand stem size would indicate likelihood that novel Gambel oak patches are likely to be vigorously growing thickets with normally distributed abundances of smaller stems (Table 1). If Gambel oak is situated to expand across the landscape, we will need to consider new management approaches that are considerate of the species' variable structural form and age dynamics as demonstrated in this study. Further aspects of Gambel oak functioning as they relate to vegetation management actions will need to be examined in case studies framed around experimental treatments since the scope of this study is observational in nature. Resulting management insight of the species in an experimental framework allows implementation of informed treatments targeted towards desired future stand conditions.

We speculate there is considerable potential for Gambel oak to be opportunistically favored in both the more extreme wet years and the more extreme dry years in different parts of its Colorado distribution. The species' growth potential is a function of fitness referencing our demographic analysis alone. The suitability of Gambel oak is reflective of the observed

productivity in concert with its advantageous traits in the xeric nature of its environment in our region of study. Its higher elevation ecotone is usually shared with ponderosa pine cover types or quaking aspen cover types and the lower elevation ecotone is shared with Pinyon/Juniper and other xeric montane shrub communities (Colorado State Forest Service, 2009). In the upper ecotone in a very dry year, Gambel oak's xeric traits situate it to better deal with droughty conditions compared to ponderosa pine and quaking aspen (Allen & Breshears, 1998). Alternatively, in an extreme wet year, at the lower elevation ecotone Gambel oak has the potential to take advantage of added moisture, rapidly taking advantage of a wet year with immediate asexual regeneration. Perhaps advantageously over its pinyon/juniper neighbors at that ecotone due to its variety of asexual growth forms, compared to the spatiotemporally explicit masting strategy in pinyon pine despite previous thought of Gambel oak facilitation to mature pinyon stands (M. E. Floyd, 1982; Wion et al., 2019). Consideration of Gambel oak's ecotones in its present distribution is worthwhile, but with changing climates, the climatic envelope of this species is liable to alter in relation to the tolerance of moving abiotic limits on the species' distribution (Harper et al., 1985; Loarie et al., 2009).

If Gambel oak's range has the potential to expand to fill a larger climatic envelope, then our understanding of the linkage between ecological response of the species and appropriate management techniques needs to be solidified. Adaptive management facilitating cover type transitions to climate change tolerant species has been a concern of this region already. If Gambel oak becomes a greater component of dominant forest cover types, we will need to identify how management action can facilitate desired forest outcomes while balancing the increasing abundance of Gambel oak. Dominant plant cover types in the Southwest's vegetation mosaic including pinyon juniper, ponderosa pine, Spruce/fir, and others, have had potential

climatically induced range expansion or contraction studies in addition to having been described in *Silvics of North America* (Burns et al., 1965; Kelly & Goulden, 2008; Shinneman et al., 2016). Gambel oak by contrast has not had formalized silvics documented in this manner and management for the species is already variable across the whole of its distribution. In the absence of that material, we can use documented traits to model treatments after the ecological analogue of unmanaged stands. Treatments that consider the uneven age structures implicit in the regeneration strategy of the species as well as the variability in productivity via CMD proxied by elevation will be key to managing Gambel oak in the future. The likely expansion of oak in the American Southwest will necessitate further managerial tools for landscapes where Gambel oak expansion threatens to depart from desired future conditions. Regardless of variable expansion scenarios, linking treatment action to demographic outcomes through experimental inquiry building on our described fundamental characteristics of Gambel oak will benefit management; adaptive or otherwise.

Since our observational study referenced functionally unmanaged stands, there are some insights into natural patterns of oak regeneration in the absence of natural or management-induced disturbance relevant to future management action. The sample population has developed the observed structures over the last 150 years at most, indicating a natural regeneration outcome of variable vertical structure. Gambel oak stands from all three strata showed heterogeneity in stand structure with increasing age. Meaning that without management action, within roughly 120 years, Gambel oak stand structure has differentiated in development on its own (Figure 6). Since on the Uncompahgre National Forest, Gambel oak outcomes are often executed with burning or mowing type management activities with the aim of reducing Gambel oak continuous cover, alternatively, no management may achieve a similar result. Regeneration is seemingly

consistent over a stand's lifetime given the increasing age proportions of a stand with increasing stand age. This would suggest that no action is needed for stands to regenerate. This finding is consistent across the range of stratified CMD values (Figure 6). Management action looking to increase structural variation in Gambel oak may be able to accelerate the rough 120-year mark of natural occurrence by implementing treatments promoting size classes as early as 30 years into the developmental SDI ratio curve. This could have the effect of creating asymmetric competition within stands thus reducing the time needed until differentiation into old growth formed stands with non-normal distributions like the stand structures observed after the 120-year mark. The natural path that Gambel oak regeneration, and consequently, stand structure follows yields variable structure. If management values variation in oak form, a no management action scenario could create heterogeneity out of Gambel oak patches that are very homogenous in the first 30 years of growth. Allowing stands to reach maturation or promoting maturation by implementing asymmetric competition earlier in a stand's lifetime provide suitable alternatives to mowing or burning Gambel oak to the end of reducing homogeneity on the landscape within this cover type.

Within the southwestern Colorado region, Gunnison Sage Grouse habitat management is a constant concern that Gambel oak management plays into (Aldridge et al., 2012; Beck et al., 2003; Braun et al., 2014). Since corridor connectivity between Gunnison Sage Grouse populations is considered an effective management goal, some areas require high management input to meet habitat needs of Gunnison Sage Grouse. Since the species is sensitive to vertical structures that inhibit it from being able to see far, maturing Gambel oak thickets taller than 1.5 meters significantly reduce quality of habitat for the Gunnison Sage Grouse (Oyler-McCance et al., 2001; Wisdom et al., n.d.). As such, in areas critical to maintaining connectivity of habitat

between disjunct populations, management action aimed at reducing standing structures via mowing is necessary. Our work has captured the general relation between stem height and age for Gambel oak across CMD conditions. As such, in this region, for meeting habitat requirements aimed at reducing vertical structure in Gambel oak for the Gunnison Sage Grouse, we could expect to reenter mowed stands on a 10-15-year interval to maintain heights below a 2.5-meter threshold (Figure 3). To maintain heights below a 1.5-meter threshold, repeated entry to critical areas with dominant Gambel oak cover could be expected in a 5-10-year interval. This relation between height and age is not uniform across CMD referenced abiotic conditions. In the high CMD conditions, the aridity seems to be slowing stem height growth. As such, the estimates for reentry into stands to maintain thresholds of vertical structures may be less frequent. Contrarily, the low CMD stands tended to achieve height more rapidly and in critical areas for Gunnison Sage Grouse management, it could warrant more frequent reentry to maintain tolerated vertical thresholds for suitable habitat.

Another management outcome tied to Gambel oak ecology is directed towards browse/acorn production for wildlife habitat value. Outside of the intolerance of Gunnison Sage Grouse towards large Gambel oak cover, many wildlife species ranging from insects to ungulates in this region rely on foraging in Gambel oak cover types. Acorn production particularly is often a desired management outcome outside of this region for wildlife habitat value (McCulloch et al., 1965; R. P. Neilson et al., 1980). Acorn production is a function of tree size, so within our Gambel oak populations, management geared towards promoting tree size by implementing size classes within oak patches could facilitate more productive cover for wildlife habitat (Abella, 2008a). In the context of this goal, the location of management action is important given the dissimilar relative growth rates described along the CMD gradient. Targeting treatments in low

CMD locations would likely provide optimum effect for increasing production given the positive increasing relation between absolute growth rate and decreasing CMD values. Implementing management action geared towards differentiating size classes in any Gambel oak patch would promote asymmetric growth and ultimately larger more acorn rich trees, however the resulting increased production following management action would likely happen more quickly in areas with high absolute growth rates (Pretzsch & Biber, 2010).

1.5 Conclusion

Fundamental characteristics of Gambel oak demography and productivity have been explored in our work highlighting variable patterns in growth and structure. The climatic variation across the scope of the study showed variable patterns in Gambel oak biometrics relevant for informed management actions. The relation between productivity expressed as relative growth rate and intraspecific competition and abiotic influences of the species have brought to light the importance of stem size, stand structure, and moisture in governing stand growth in the Colorado context of the species' distribution. These patterns of Gambel oak traits have built a foundational understanding of the species' biometrics that lend utility to achieving desired Gambel oak management outcomes. While we are limited by the observational nature of this study, we have documented an uneven age structure in Gambel oak with evidence for continued regeneration beyond the point of establishment for a stand. This facilitates the idea that no action treatments could allow for regeneration and eventually heterogeneous size differentiation given time, and that this could be accelerated with implementation of treatments aimed at promoting variation in size classes. Additionally, management goals oriented toward growth and greater tree size will yield more rapid results in areas with lower CMD. Gambel oak is categorically dissimilar within our stratified sample population for all demographic metrics

exempting age proportion indicating systematic difference of biomass accumulation and density/stocking across a landscape scale gradient of moisture availability. This set of observational findings necessitates further exploration of experimental treatments. While the patterns of demography and productivity exemplify the variable form and structure of Gambel oak, effectiveness of management action with respect to climatic condition and stand structure modification needs to be investigated further.

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